BPA Contract #99-041-00

Utilization of Nitrogen from Spawning Salmon by Juvenile Chinook Salmon and Steelhead in Two Tributaries of the Columbia River

Final Report

Prepared By
Robert E. Bilby[1], Todd Bennett and Phil Roni
National Marine Fisheries Service
Northwest Fisheries Science Center
2725 Montlake Blvd. E.
Seattle, WA 98115

Prepared For

Linda Catabay, Contracting Officer
Bonneville Power Administration…
Portland, Oregon

April 2002

[1] Current address: Weyerhaeuser Co., Technology Center 1A5, PO Box 9777, Federal Way, WA 98063

Abstract

We utilized nitrogen (N) stable isotope ratios of muscle tissue from juvenile chinook salmon and steelhead collected at 25 sites in the Salmon River and John Day River watersheds to evaluate the extent to which N from spawning salmon was utilized by the young fish. By comparing N stable isotope ratios between juvenile anadromous fishes and resident trout located upstream from a barrier to salmon passage, we found evidence of salmon-derived N in juvenile chinook at 24 of the 25 sites and at 17 of the 25 sites for steelhead. N stable isotope ratios in the juvenile anadromous fish were too high at most of the sites to be accounted for simply by contributions of salmon-derived N from the egg, indicating dietary incorporation of this material. Biomass of juvenile anadromous salmonids was positively related to the abundance of carcass material deposited at a location, suggesting that the spawning salmon may be influencing aquatic productivity and hence, the food availability for the rearing fishes. The amount of carcass material deposited at our study sites was low; never over 15 g/m^2. These deposition rates are estimated to be about 1% of the historical rate in these watersheds. Nonetheless, we estimate that up to 20% of the N in the muscle tissue of the juvenile fish was contributed by spawning salmon. Thus, even at the currently depressed levels of salmon returns to the Columbia River Basin, salmon do make a measurable contribution to N availability in streams. This suggests that even modest increases in salmon escapement may enhance the capability of freshwater systems to support juvenile salmon and trout.

Pacific salmon transport large quantities of organic matter in the form of carcasses and eggs from the North Pacific Ocean to aquatic ecosystems where they spawn and die (Larkin and Slaney 1997; Gresh et al. 2000). Salmon eggs and carcasses are eaten by birds, mammals, fish and invertebrates and the nutrients released by the decomposing carcasses can stimulate plant and microbial production that subsequently increases invertebrate production resulting in increased food availability for fish (Naiman et al. *in press*).

The ecological significance of materials deposited by spawning salmon for aquatic ecosystems has been well established over the last decade. Juvenile salmon and trout readily ingest carcass flesh and eggs of spawning salmon (Kline et al. 1990; Bilby et al. 1996). Fishes with access to this material exhibit higher growth rates than fish at locations with few spawning salmon (Bilby et al. 1998). Increases in the body size of juvenile salmonids can significantly increase their survival. Larger body size has been positively correlated with overwinter survival in freshwater and marine survival of juvenile coho salmon and steelhead (Bilton et al. 1982; Ward and Slaney 1988; Hartmann and Scrivner 1990; Holtby et al. 1990; Quinn and Peterson 1996; Tipping 1997).

The ecological significance of the nutrient and organic subsidy provided by spawning salmon has been demonstrated for coastal watersheds in the Pacific Northwest and Alaska (Kline et al. 1990; Bilby et al. 1998). However, the influence of this material on the productivity of watersheds in arid areas of the interior Pacific Northwest has been less well studied (Johnson et al. 1997) and no evaluation of this process has been conducted on the interior Columbia Basin. In addition, the length of time marine nutrients are retained in streams has not been well documented.

The numbers of adult salmon spawning in streams throughout Washington, Oregon, Idaho and California has been severely reduced over the last century (Nehlsen et al. 1991). Gresh et al. (2000) estimated that the current contribution of salmon-derived biomass and nutrients is less than 2% of that historically delivered to watersheds tributary to the Columbia River. If salmon make an important contribution to the availability of nutrients in these systems, the decline in returning fish over that last 150 years may have greatly impacted the capacity of these systems to support juvenile salmonids and other aquatic biota.

We used nitrogen (N) stable isotope ratios to examine the utilization of salmon-derived N by juvenile stream-type chinook salmon and steelhead in tributaries of the Salmon River watershed in Idaho and the John Day River watershed in Oregon. The objectives of this study were to:

1) Determine the extent to which salmon-derived N is found in the muscle tissue of juvenile stream-type chinook salmon and steelhead during summer, prior to arrival of adult salmon.
2) Determine if the amount of carcass tissue deposited at a site and the level of salmon-derived N in the tissues of juvenile fish are related.
3) Determine if there is a relationship between carcass abundance and the biomass of juvenile salmonids rearing at that site.

Methods

Study Sites

Sampling was conducted on stream reaches in the Salmon River watershed in central Idaho and the John Day River watershed in northeastern Oregon (Figure 1). The Salmon River is a major tributary of the Snake River draining over 36,000 km^2 . This watershed exhibits large variations in elevation, from 296 m to 3,717 m above sea level, which produces a wide range in precipitation (13 to 250 cm annually) and air temperature (-4 to +11°C mean annual) (Daly et al. 1994; Thornton et al. 1997). As a result of the variation in physical conditions, natural vegetation ranges from alpine forests to arid grassland. The basin is sparsely populated and logging, mining, livestock grazing and irrigated agriculture are the dominant land uses. The Bureau of Land Management and the U.S. Forest Service manage about 90% of the land in the basin with approximately 27% designated as wilderness area. Anadromous salmonids in the Salmon River basin include spring/summer and fall chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*), and steelhead (*O. mykiss*). All of these stocks have been listed as threatened or endangered under the Endangered Species Act (National Marine Fisheries Service 1991; 1992; 1997).

The John Day River drains an area of north-central Oregon and flows into the Columbia River downstream from the confluence of the Columbia and Snake rivers (Oregon Water Resources Department 1986). This watershed is smaller than the Salmon, draining about 21,000 km^2. The river originates in the mountainous southern portion of the basin where elevations reach about 2500m and flows northward to the Columbia River. Mean annual temperatures in the watershed range from $4^{o}C$ to $11^{o}C$ and precipitation from 23 cm to

102 cm, varying with elevation. Vegetation varies with changes in climate and elevation from forest at higher elevations to sagebrush and perennial grasses lower in the basin. Land use is similar to the Salmon River watershed with grazing, forestry and irrigated agriculture the predominant activities. In contrast to the Salmon River, however, only about 37% of the land in the John Day River watershed is federally managed, mostly in the mountainous headwaters. The John Day River supports runs of spring/summer chinook salmon and steelhead, all of which have been listed as threatened under the federal Endangered Species Act (National Marine Fisheries Service 1992; 1997).

<u>Stable Isotope Analysis</u>

The relative contribution spawning salmon make to the nutrient pool in freshwater ecosystems can be quantified using N stable isotope analysis (Kline 1990; 1994; Bilby et al. 1996; 1998; Johnston et al. 1997). Spawning salmon contain higher proportions of the heavier isotopic form of N (^{15}N) than does N delivered to the stream from other sources (Kline et al. 1990; Bilby et al. 1996). As a result, N stable isotope ratios provide an indication of the proportion of N of marine origin in a sample collected from the stream.

N stable isotope ratios are expressed as $\delta^{15}N$ values (Peterson and Fry 1987). These values represent the difference in the ratio of ^{15}N to ^{14}N in a sample and the ratio in air. Values are calculated:

$$\delta^{15}N = [(R_{sample} - R_{standard})/R_{standard}] \times 1000$$

where R_{sample} = the ratio of $^{15}N/^{14}N$ in the fish tissue sample and $R_{standard}$ = the ratio of $^{15}N/^{14}N$ in atmospheric N (Peterson and Fry 1987). Units for $\delta^{15}N$ values are parts per mil (‰) with higher values indicating higher proportions of the salmon-derived N in the sample.

Muscle tissue samples were collected from juvenile chinook salmon, juvenile steelhead, resident trout and chinook salmon carcasses. The sample collection protocol is described below. Preparation of the muscle tissue samples for stable isotope analysis involved freeze-drying the tissue and grinding the dried material to a fine powder with a ball grinder and mortar and pestle. Prepared samples were sent to the University of Alaska, Fairbanks for stable isotope analysis. Approximately 1-1.5 mg of the ground, dried tissue was combusted, and the evolved N_2 gas was introduced into a continuous flow, isotope ratio mass spectrometer to determine $\delta^{15}N$ values.

Sampling

Juvenile chinook, juvenile steelhead and resident trout were sampled at 18 sites in the Salmon River watershed and 10 sites in the John Day River watershed during the summers of 1999 and 2000 (Table 1). Sampling at each site included the collection of tissue samples for stable isotope analysis and the determination of density and body size of juvenile chinook salmon and steelhead. A Smith-Root Model 12-B backpack electrofisher was used to collect fish. We attempted to collect approximately 20 juvenile chinook salmon and from 10 to 20 juvenile steelhead at each site. Approximately 20 resident rainbow trout or brook trout were collected from stream reaches that were not accessible to anadromous fish nearby the sampled reaches containing anadromous species. All fish were narcotized with MS-222 prior to measuring and weighing. The fish were weighed to the nearest 0.1g, measured for total length. Those fish retained for isotope samples were euthanized with an overdose of MS-222, then placed in plastic bags and stored on dry ice for transport back to the lab. Fish not retained for isotope analysis were returned to the stream after they had recovered from the anesthetic.

Juvenile salmon, steelhead and trout were sampled prior to the arrival of adult salmon at all sites in the John Day River watershed and most of the sites in the Salmon River watershed. At a few sites in the Salmon River, a few carcasses from early arriving fish were present at the time samples were collected, but all collections were complete before large numbers of adult salmon arrived at these sites. Thus, nearly all the salmon-derived N in the tissues of the sampled juvenile fish originated from material deposited by salmon spawning in years previous to the study and retained in the system. Nearly all the sampled juvenile chinook and most of the steelhead used for stable isotope analysis were mortalities associated with a chinook salmon PIT(passive integrated transponder)-tagging project managed by the National Marine Fisheries Service. Supplemental sampling was required at some sites to capture a sufficient number of juvenile steelhead (collection permits: NMFS ESA Section 10 for Snake River chinook and steelhead - #1056; USFWS Bull trout consultation – Reference # 1-7-00-F-336). A total of 454 chinook salmon, 298 steelhead and 138 resident trout were collected for stable isotope analysis (Table 2).

Resident trout were collected to determine the N stable isotope value of fish with no access to salmon-derived N. Ideally, these trout would have been collected above an impassable barrier upstream from each location where the anadromous fishes were sampled. However, this was not possible due to several problems. Bull trout (*Salvelinus confluentus*), a species listed under the federal Endangered Species Act, were frequently abundant above passage barriers on many of the streams we sampled. Our collection permit required us to stop electrofishing at a site when six bull trout had been observed. As a result, it was impossible to obtain a sufficient number of rainbow trout (*O. mykiss*) or brook trout (*S. fontinalis*). At other sites there were no obvious barriers to anadromous fish passage. Thus, resident trout collected at these sites could not be assumed to be free of salmon-derived nutrients. We were able to locate five sites in the Salmon River watershed and two in the John Day River watershed above barriers where we were able to collect a sufficient number of trout. Values for juvenile salmon and steelhead were compared with the values for resident trout collected closest to the anadromous fish sample location (Table 1).

Muscle tissue samples also were collected from the carcasses of post-spawning chinook salmon for stable isotope analysis. These samples were collected during redd surveys conducted by the Idaho Department of Fish and Game, the Oregon Department of Fish and Wildlife, the U.S. Forest Service, the Nez Perce Tribe and the Shoshone-Bannock Tribe. A 25-g chunk of muscle tissue was excised from below the dorsal fin of each carcass, and length, sex, and weight of each carcass was recorded. Samples were obtained from a total of 340 chinook salmon carcasses. All samples were stored on ice in the field and frozen as soon as possible. Carcass samples were collected at multiple locations in both the Salmon River and John Day River watersheds. The low returns of chinook salmon to the Salmon River during the year sampled (1999) and the difficulty in accessing some sites prevented collection of carcass tissue samples from several locations where juvenile fish were sampled. In these cases carcass samples were collected from locations as close to the study sites as possible. Carcass tissue samples were obtained for all sample sites in the John Day River (Table 1).

Abundance of juvenile chinook and steelhead was determined at most sites by snorkeling three, 100-meter reaches at each sampling site. Snorkel surveys were performed by two divers moving upstream abreast of one another identifying and counting all fish encountered. As our sampling permit prohibited activities in the stream when adult salmon were present, it was not possible to snorkel three reaches at all locations. When adult salmon were observed, sampling was terminated until the fish passed through. In cases when the adult fish did not leave, the section was not sampled. However, this restriction affected sampling at only four sites in the Salmon River (1 section per site) and no sites in the John Day River. No abundance estimate could be made at the East Fork Salmon River site as the owner of the adjoining land denied access for this purpose. However, the National Marine Fisheries Service PIT-tagging crew was able to access the site and provided samples for stable isotope analysis.

Data Analysis

Higher $\delta^{15}N$ values in the juvenile salmon and steelhead than in the resident trout at a site was considered to be indicative of incorporation of salmon-derived N in the juvenile fish. We compared $\delta^{15}N$ values among chinook salmon, steelhead and resident trout using a one-way ANOVA. When significant differences were identified ($p< 0.05$) multiple comparisons of means were made using a Tukey Test (Zar 1999 (fourth edition)).

Because variation in the $\delta^{15}N$ values of carcasses and resident trout among sites was high, the $\delta^{15}N$ values of the juvenile salmon and steelhead do not directly indicate their level of salmon-derived N. Therefore, we estimated the proportion of salmon-derived N in the tissues of the juvenile chinook and steelhead at each site. This calculation followed a method used in other studies (Kline et al. 1990; Bilby et al. 1996; Helfield and Naiman 2001). In order to estimate this value, some assumptions about the pathways of N incorporation by the juvenile fish were necessary as the process of trophic exchange influences $\delta^{15}N$ values due to isotopic fractionation (Peterson and Fry 1987). As the juvenile fish were sampled prior to the arrival of most adult salmon: direct consumption of carcass flesh and eggs by the young fish was not an important mechanism of uptake. Thus juvenile chinook salmon and steelhead we sampled obtained much of the salmon-derived N they contained by eating invertebrates that had ingested plant material containing salmon-derived N. In order to estimate the proportion of salmon-derived N, it is necessary to account for isotopic enrichment that occurs as a result of fractionation during trophic exchanges. In our estimate we assumed no fractionation as a result of autotrophic uptake, which is generally the case in situations where N is in limited supply (Peterson and Fry 1987). We then assumed a fractionation rate of 3‰ as invertebrates ate the plant material and another 3‰ due to consumption of the invertebrates by the fish (Minigawa and Wada 1984). Thus, a juvenile salmon ingesting invertebrates that contain only N obtained from salmon carcasses would exhibit a $\delta^{15}N$ value 6‰ higher than the salmon carcasses. This assumption of two trophic exchanges ignores the fact that some predatory insects are consumed by the fish, which involves an additional trophic exchange and further elevates the isotopic value of the fish. Thus, we likely slightly overestimate the actual proportion of salmon-derived N in the juvenile fishes. The proportion of salmon-derived N is computed as:

$(\delta^{15}N \text{ juvenile salmon} - \delta^{15}N \text{ resident trout}) / ((\delta^{15}N \text{ carcass}+6‰) - \delta^{15}N \text{ resident trout})$.

Density and average body weight values were used to calculate juvenile salmonid biomass at each study site. Average body weights were based on the weights of the fish collected during the PIT tagging operation and densities were determined by the snorkel surveys. The biomass values were regressed against carcass deposition rates to explore the hypothesis that the amount of carcass tissue delivered to a site has an influence on the productivity of that site.

Results

Deposition of carcass tissue at the Salmon River study sites ranged from zero at Herd Creek to over 14 g/m^2 at the South Fork Salmon River site (Figure2). Deposition was similar at the John Day River sites, ranging from less than 1 g/m^2 at site 2 on the mainstem of the John Day River to 11.6 g/m^2 at site 3 on the Middle Fork of the John Day River. The $\delta^{15}N$ values of the chinook salmon carcasses varied somewhat among sites, ranging from about 13‰ to 15‰ (Figure 3).

The $\delta^{15}N$ values of juvenile salmon and steelhead indicated that N derived from adult salmon had been incorporated into the tissues of the young fish (Table 2). Juvenile chinook salmon exhibited $\delta^{15}N$ values greater than those for resident trout at all sites in both the Salmon River and John Day River watersheds except one (Secesh River). Steelhead $\delta^{15}N$ values were greater than those for resident trout at 9 of the 14 Salmon

River sites and 8 of the 9 John Day River sites. Chinook salmon displayed higher $\delta^{15}N$ values than steelhead at four Salmon River sites and six John Day River sites.

The proportion of salmon-derived N in the juvenile chinook salmon and steelhead at those sites where we found a significant difference in $\delta^{15}N$ values between anadromous and resident fishes ranged from less than 2% to about 20% (Figure 4). However, at a majority of the sites chinook contained from 5% to 15% salmon-derived N and steelhead from 4% to 12%. Chinook salmon consistently contained higher proportions of salmon-derived N than steelhead.

The amount of carcass material deposited at a site could influence the amount of salmon-derived N available at the site. In other studies this relationship has been observed as amount of carcass material deposited at a site has been related to the level of salmon-derived N in the tissues of juvenile fish (Bilby et al. 2001) and insects (Johnston et al. 1997). However, the level of enrichment with salmon-derived N in juvenile chinook salmon and steelhead was not related to the amount of carcass tissue deposited at our study sites (Figure 5a and 5b).

Juvenile chinook salmon densities at the Salmon River sample sites ranged from 0.001 fish/m^2 in Loon Creek to 0.420 fish/m^2 in the South Fork Salmon River. Chinook salmon densities at the John Day River sites were comparable to the Salmon River sites, ranging from 0.016 to 0.181 fish/m^2. Steelhead densities were generally lower than juvenile chinook salmon but especially so at the Salmon River sites, where steelhead densities never exceeded 0.006 fish/m^2. Steelhead densities at the John Day River sites were considerably higher than those at the Salmon River sites, ranging from 0.007 to 0.096 fish/m^2.

Weight of the juvenile fish also varied among sites, especially for steelhead. Average weight of chinook salmon ranged from 3.0 g to 5.6 g at the Salmon River sites. Juvenile chinook at the John Day River sites ranged in weight from 3.6 g to 7.6 g. Average steelhead weights were much more variable among sites due in part to the presence of at least 2 age classes and the unequal representation of the age classes among sites. For example, the vast majority of the steelhead captured at Loon Creek in the Salmon River were less than 80mm total length and 5 g in weight. In contrast, all the steelhead captured at the Herd Creek site except one were over 100 mm in length and weighed more than 15 g. Average steelhead weights at the Salmon River sites ranged from 5.1 g to 23.8 g and from 8.6 to 19.0 g at the John Day River sites.

Biomass of juvenile chinook and steelhead was computed for each site from the density and average weight values (Figure 6). Generally, steelhead comprised a smaller proportion of the biomass at the Salmon River sites. At the John Day River sites, steelhead were a much larger contributor to the total biomass value accounting for more than 50% at 5 of the 9 sample sites and accounting for at least 30% of the biomass at all locations. Total juvenile salmonid biomass increased with increased abundance of carcass material deposited at a site the previous autumn (Figure 7; $p<0.05$).

Discussion

The $\delta^{15}N$ values for salmon carcasses were well above those of non-marine N sources, as evidenced by the isotope values of the resident trout (Table 2). The $\delta^{15}N$ value of an organism is higher than that of its food source due to the process of isotopic fractionation (Peterson and Fry 1987). Therefore, the resident trout we sampled were likely consuming food items with $\delta^{15}N$ values of 3.5‰ to 4.5‰ , assuming a fractionation rate of 3‰ (Minigawa and Wada 1984). The high degree of distinction between the N stable isotope value of non-salmon influenced food sources in the system and the $\delta^{15}N$ value of the carcasses made the $\delta^{15}N$ values of the juvenile salmon and steelhead highly responsive to the incorporation of salmon-derived N.

The elevated $\delta^{15}N$ values of juvenile salmon and steelhead relative to resident trout at our study sites clearly indicates that the juvenile anadromous fishes in these two, large tributaries of the Columbia River contain N derived from adult salmon. Without direct access to adult carcasses, the juvenile fishes can obtain this material from two sources. Some of this salmon-derived N is transferred to the young fish during embryo development. Another possible source is salmon-derived N that is incorporated into the trophic system of the stream and passed to the young fish through their diet. Salmon-derived N passed from adult to juvenile fish through the egg is of little ecological significance. However, if nutrients deposited by the spawning salmon are incorporated into the trophic system of the stream, these nutrients may play a role in stimulating the biological productivity of the stream and increase the capacity of the site to support juvenile salmon and other fishes.

If incorporation of salmon-derived N occurred only during egg incubation, the $\delta^{15}N$ values of the young fish would decrease after emergence from the gravel as the marine N was diluted by N from sources with lower $\delta^{15}N$ values. We estimated the stable isotope value that the juvenile chinook and steelhead would have exhibited if no salmon-derived N was included in the diet of the fish, assuming an initial weight of 0.35g for chinook salmon and 0.30g for steelhead (Figure 8A; 8B). Initial $\delta^{15}N$ values for the fry were assumed to be equal to the isotopic value of the carcasses at that location (Figure 3). $\delta^{15}N$ value of food not influenced by salmon-derived N was estimated from the resident trout values (Tab. 2) reduced by 3‰ to account for isotopic fractionation (Minigawa and Wada 1984). This analysis indicated that the $\delta^{15}N$ values of the salmon and steelhead at most of our sites were too high to be attributed only to salmon-derived N from the egg. At those sites where the anadromous fish exhibited a significantly higher $\delta^{15}N$ value than resident trout (Table 2), salmon-derived N obtained during embryonic development was sufficient to cause the observed isotopic value in juvenile chinook at only 4 sites: Bear Valley, Elk, Big and Granite creeks. For steelhead dietary incorporation of salmon-derived N was apparent at all sites except Elk Creek. At all other locations the discrepancy between the isotopic ratio that would have been produced simply by dilution of the salmon-derived N from the egg and the actual measured value was large. These data indicate that salmon-derived N, and likely other nutrients, are incorporated into the trophic system of the stream and transferred to the invertebrates consumed by the rearing salmon and steelhead.

The lack of a relationship between proportion of salmon-derived N and the amount of carcass tissue deposited at a site (Figure. 5A; 5B) differs from the situation observed in other studies. Several studies have demonstrated that the proportion of salmon-derived N in stream biota is related to the density of salmon spawning at that site. In tributaries to the Stuart River in British Columbia the proportion of salmon-derived N in insects and juvenile fishes increased with increasing numbers of spawning sockeye salmon (Johnson et al. 1997). In coastal Washington streams supporting coho salmon, increasing densities of spawning fish was positively associated with increased $\delta^{15}N$ levels in coho salmon fry (Bilby et al. 2001). The level of salmon-derived N increases rapidly as availability of carcass tissue increases at low and moderate levels of deposition and increases at a much slower rate at high carcass densities. No such pattern was seen at the Salmon River and John Day River sites in this study. However, the studies noted above examined sites where the amount of carcass tissue deposited was far greater than even the site with the highest level of deposition in this study. Bilby et al. (2001) examined sites receiving inputs of coho salmon carcass material up to 756 g/m^2. Deposition of sockeye salmon carcass tissue at the Fraser River sites examined by Johnston et al. (1997) exceeded 2000 g/m^2 at some sites. In contrast, the site receiving the greatest amount of carcass tissue in this study was the South Fork Salmon River with 14.6 g/m^2. Bilby et al. (2001) noted a considerable amount of variation in the level of salmon-derived N in juvenile coho salmon at very low levels of carcass deposition. Thus, the absence of a relationship between level of isotopic enrichment in the juvenile salmon and amount of carcass tissue deposited at a site in this study is likely due to the limited range of carcass deposition rates we examined. Unfortunately, levels of carcass deposition from wild salmon in the interior Columbia River Basin were severely depressed during our study, precluding the option of sampling sites with high rates of carcass input.

The proportion of salmon-derived N in the muscle tissue of juvenile salmon and steelhead observed in this study was well below the levels observed at other locations. At sites in the Pacific Northwest with high levels of carcass abundance, the proportion of salmon-derived N in juvenile salmonids often exceeds 30% (Bilby et al 1996; 1998) and can approach 100% in situations with extremely high levels of deposition (Kline et al. 1990). In this study, the proportion of salmon-derived N in juvenile chinook and steelhead at the sites where the $\delta^{15}N$ value of the anadromous fishes was significantly greater than the resident trout (Tab. 2) ranged from less than 2% to about 20%. Thus, the proportion of salmon-derived N in juvenile salmon seen in other studies has generally been higher than the upper end of the range in our study. It is surprising, however, that the levels of salmon-derived N we observed were as high as they were given the fact that carcass availability was an order of magnitude lower, or more, than the deposition rates observed in some other studies. The high efficiency of incorporation of salmon-derived N at the Salmon River and John Day River sites indicates that salmon-derived nutrients are readily utilized when available and that retention of these nutrients is high.

Although it is evident that salmon-derived N is present at many of the sites we examined, this fact does not indicate that this nutrient subsidy influences biological productivity. We attempted to examine this question by comparing juvenile salmonid biomass to amount of carcass deposited at a site. Biomass was considered the most appropriate parameter for evaluating the effect of carcass deposition on site productivity. Evaluating the effect of salmon carcass nutrients on productivity by examining fish density is complicated by the fact that carcass abundance the previous autumn may be directly related to the deposition of eggs at a site; more eggs produce more fry. Thus, density alone cannot provide an indication of any enhancement in site productivity related to carcass deposition. Growth rate of individual fish also is affected by density, as both the productivity of a site (food availability) and the number of fish competing for the food influence growth rate. These problems are reduced if biomass levels at each site are related to amount of carcass deposited (Figure 7). By combining density and weight into an estimate of biomass the effects of initial population size are diminished as density is inversely related to weight of individual fry as long as food is in limited supply. We had no empirical evidence from our sites that food was limiting growth or production of juvenile salmonids. However, average stomach fullness of salmon and trout in the Yakima River watershed, another Columbia River tributary, rarely exceeded 30% during the summer and fall of 1998 and 1999 when densities of salmon were very low, suggesting food availability is limiting fish growth in this system (James et al. 1999).

We did observe a weak, albeit significant, relationship between biomass and carcass deposition (Figure 7). This relationship suggests that the carcasses may be having an effect on biological productivity at our study sites. However, many other factors also may influence biomass of juvenile salmon and trout. Physical habitat conditions, water temperature and availability of nutrients from sources other than spawning salmon all can affect biomass of fishes rearing at a site, and these features did vary among the sites we examined. , The increase in biomass of juvenile salmonids with increasing rates of carcass deposition does, however, suggest that the nutrient subsidy being provided by spawning salmon may be an important factor in determining the capacity of these sites to support juvenile salmon and steelhead.

This research indicates that the nutrient subsidy provided by spawning salmon may influence the capacity of freshwater habitats to support juvenile salmonids in watersheds of the interior Columbia River Basin. We found clear evidence of salmon-derived N in the muscle tissues of juvenile chinook salmon and steelhead. It was evident that a substantial amount of the salmon-derived N was being incorporated by the young fish through their diet, suggesting that the productivity of the system may be influenced by the nutrient contribution from the spawning adults. The potential influence on productivity also was suggested by the relationship we observed between the biomass of juvenile salmonids at a site and the amount of carcass tissue delivered to that location the previous autumn.

Historically, returning salmon transported from 76,000 to 100,000 mt of organic matter annually into the Columbia River, including 635 - 750 mt of N and 75 - 90mt of phosphorus (Gresh et al. 2000). Levels of input through the 1970s, 1980s and early 1990s were between 0.8% and 2.0% of the historic values. Given the levels of salmon-derived N in juvenile salmon and steelhead that we observed, even at these very low escapement levels salmon-derived nutrients may be of critical importance in maintaining the productivity of Columbia River tributaries.

In 2001 salmon returned to the Columbia River in numbers not seen since the 1930s. This large return was attributed to productive ocean conditions and favorable river flow conditions at the time the young fish of this cohort were rearing and migrating down the Columbia River (Pers. comm., T. Unterwegner, ODFW). If these higher levels of escapement persist for several years, there will be an opportunity to examine the effect of increased deposition of carcass tissue on the productivity of freshwater habitats in the Columbia River watershed. Collection of these data should help to quantify the relationship between numbers of spawning salmon and the nutritional health of the habitats where the young fish rear. As the productive potential of aquatic systems is as much a component of habitat quality as physical characteristics, understanding this relationship may be of key importance in determining how to restore salmon habitat in the Columbia River Basin most efficiently and effectively.

ACKNOWLEDGEMENTS:

This study was made possible through funding by the Bonneville Power Administration. Thanks are due to Stephen Achord, Melissa Boles, Kevin Kumagai, Greg Bary, Peter Johnsen, Patricia Garcia, Brian Sodeman, and many others for sample collection and preparation. The Idaho Dept. of Fish and Game, Oregon Dept. of Fish and Wildlife, the Shoshone-Bannock, Warm Springs, and Nez-Perce Tribes were instrumental for site selection and carcass collections. Thanks also to Norma Haubenstock of the University of Fairbanks, AK, for sample processing, and Cara Campbell (USGS) for providing Figure 1.

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Table 1: Carcass and resident trout $\delta^{15}N$ values used at each site to calculate relative enrichment values and % marine-derived N. The resident trout $\delta^{15}N$ value associated with each site where anadromous fishes were used to determine if the anadromous fish were utilizing N from spawning salmon. These comparisons are shown in Table 2.

Juvenile Fish Sample Site	Carcass Values	Resident Trout Values
Salmon River Basin		
Bear Valley Cr.	Bear Valley Cr.	Cape Horn Creek
Elk Cr.	Bear Valley Cr.	Cape Horn Creek
Sulphur Cr.	Bear Valley Cr.	Cape Horn Creek
Marsh Cr.	Bear Valley Cr.	Cape Horn Creek
Cape Horn Cr.	Bear Valley Cr.	Cape Horn Creek
Valley Cr.	Valley Cr.	Valley Creek
Loon Cr.	Bear Valley Cr.	Cape Horn Creek
Camas Cr.	Bear Valley Cr.	Cape Horn Creek
Herd Cr.	Sawtooth Hatchery	Cape Horn Creek
E. Fork Salmon R.	Lemhi River	Nethker Creek
S. Fork Salmon R.	S. Fork Salmon R.	Goat Creek
Secesh R.	Secesh R.,	Nethker Creek
Lake Cr.	Lake Cr.	Nethker Creek
Big Cr.	Big Cr.	Willow Creek

John Day River		
Mid. Fork John Day R.1	Mid. Fork John Day	Bridge Creek
Mid. Fork John Day R. 2	Mid. Fork John Day	Bridge Creek
Mid. Fork John Day R. 3	Mid. Fork John Day	Bridge Creek
North Fork John Day R. 1	North Fork John Day	Bridge Creek
North Fork John Day R. 2	North Fork John Day	Bridge Creek
North Fork John Day R. 3	North Fork John Day	Bridge Creek
Granite Cr.	Granite Creek	Bridge Creek
Mainstem John Day R.1	Mainstem John Day	Canyon Creek
Mainstem John Day R. 2	Mainstem John Day	Canyon Creek

Table 2. $\delta^{15}N$ values for juvenile chinook salmon, juvenile steelhead and resident trout from the stream sampled in the Salmon River and John Day River basins in Idaho and Oregon, respectively. Values for resident trout are for fish captured in areas that did not contain anadromous fishes. Values are shown ± one standard error followed by the number of fish in the sample. Differences in $\delta^{15}N$ values differ significantly among the fish (ANOVA, $p < 0.05$). Superscript letters indicate significant differences between means at each site (Tukey Test; $p<0.05$). [a] – Both chinook and steelhead values are greater than resident trout; [b] – chinook values only are greater than resident trout; [c] – chinook values are greater than steelhead.

Stream	Chinook	Steelhead	Resident Trout
Salmon River Basin			
Bear Valley Cr.[a]	8.14 ± 0.93 (10)	8.01 ± 0.43 (10)	
Elk Cr.[b]	8.13 ± 0.76 (8)	7.69 ± 0.42 (10)	
Sulphur Cr.[a]	8.72 ± 0.84 (13)	8.23 ± 0.23 (20)	
Marsh Cr.[a,c]	9.66 ± 0.48 (9)	8.76 ± 0.38 (7)	
Cape Horn Cr.[a.c]	9.89 ± 1.51 (8)	8.58± 0.15 (6)	7.28 ± 0.73 (16)
Valley Cr.[a]	9.59 ± 0.38 (29)	9.03 ± 0.47 (10)	6.58 ± 0.27 (20)
Loon Cr.[b,c]	8.82 ± 0.92 (29)	7.78 ± 0.73 (10)	
Camas Cr.[a]	8.91 ± 0.53 (28)	8.52 ± 0.39 (10)	
Herd Cr.[a]	9.00 ± 0.25 (8)	9.17 ± 0.67 (8)	
E. Fork Salmon R.[b]	7.29 ± 0.60 (56)	7.17 ± 0.16 (2)	
S. Fork Salmon R.[b,c]	8.28 ± 0.98 (15)	6.92 ± 0.45 (10)	

Secesh R.	7.02 ± 0.46 (14)	5.92 ± 0.40 (10)	
Lake Cr.[a]	7.68 ± 0.35 (24)	7.23 ± 0.23 (10)	
Big Cr.[b]	7.35 ± 0.73 (7)	6.86 ± 0.30 (9)	
Willow Cr.			6.59 ± 0.27 (21)
Goat Cr.			6.43 ± 0.67 (20)
Nethker Cr.			6.54 ± 0.57 (19)
John Day Basin			
Mid. Fork John Day R.1[a,c]	7.99 ± 0.34 (20)	7.05 ± 0.77 (20)	
Mid. Fork John Day R. 2[a,c]	7.45 ± 0.41 (20)	7.00 ± 0.51 (21)	
Mid. Fork John Day R. 3[a]	7.35 ± 0.37 (20)	7.01 ± 0.57 (19)	
N. Fork John Day R. 1[a]	7.96 ± 0.40 (20)	7.76 ± 0.35 (20)	
N. Fork John Day R. 2[a]	8.13 ± 0.26 (20)	7.77 ± 0.33 (10)	
N. Fork John Day R. 3[a,c]	8.14 ± 0.42 (20)	7.40 ± 0.90 (5)	
Granite Cr.[b.c]	7.22 ± 0.61 (40)	5.86 ± 0.60 (37)	
Mainstem John Day R.1[a,c]	9.10 ± 0.40 (20)	8.15 ± 0.51 (14)	
Mainstem John Day R. 2[a,c]	9.18 ± 0.34 (16)	8.72 ± 0.34 (20)	
Bridge Cr.			6.38 ± 0.82 (20)
Canyon Cr.			7.28 ± 0.54 (20)

Figure Captions

Figure 1: Map of the study areas.

Figure 2: Carcass abundance during the autumn preceding the summer when juvenile chinook salmon and steelhead were sampled.

Figure 3: $\delta^{15}N$ values for muscle tissue samples from chinook salmon carcasses. Error bars indicate +1 standard error.

Figure 4: Proportion of salmon-derived N in the muscle tissue of juvenile chinook salmon and steelhead at those sites where there was a significant difference in $\delta^{15}N$ value between the anadromous fish and resident trout.

Figure 5 A: Proportion of salmon-derived N in juvenile chinook salmon as a function of carcass biomass deposition. B: Proportion of salmon-derived N in juvenile steelhead as a function of carcass biomass deposition.

Figure 6: Juvenile chinook salmon and steelhead biomass at each of the study sites.

Figure 7: Juvenile salmonid biomass as a function of amount of carcass tissue deposited at each site. Regression statistics: biomass = 0.06(carcass deposition) + 0.21; $r^2 = 0.30$; $p<0.05$.

Figure 8A: Measured $\delta^{15}N$ values in juvenile chinook salmon and the $\delta^{15}N$ value that these fish would have displayed at each site if the only transfer of salmon-derived N to the young fish was from the egg. Comparisons are provided only for those sites where there was a significant difference between the $\delta^{15}N$ value of the chinook salmon and the resident trout. B: Same comparison for juvenile steelhead.

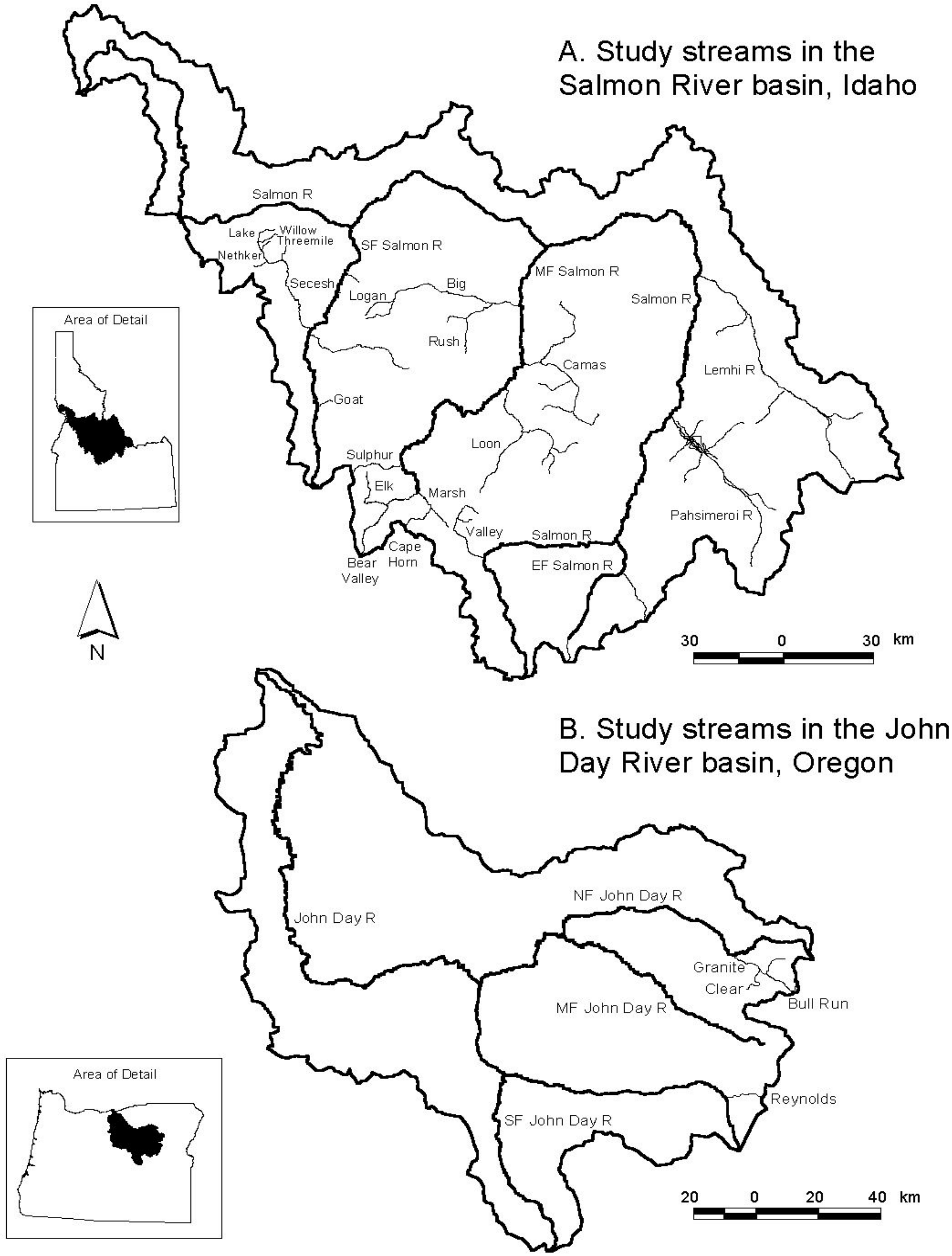
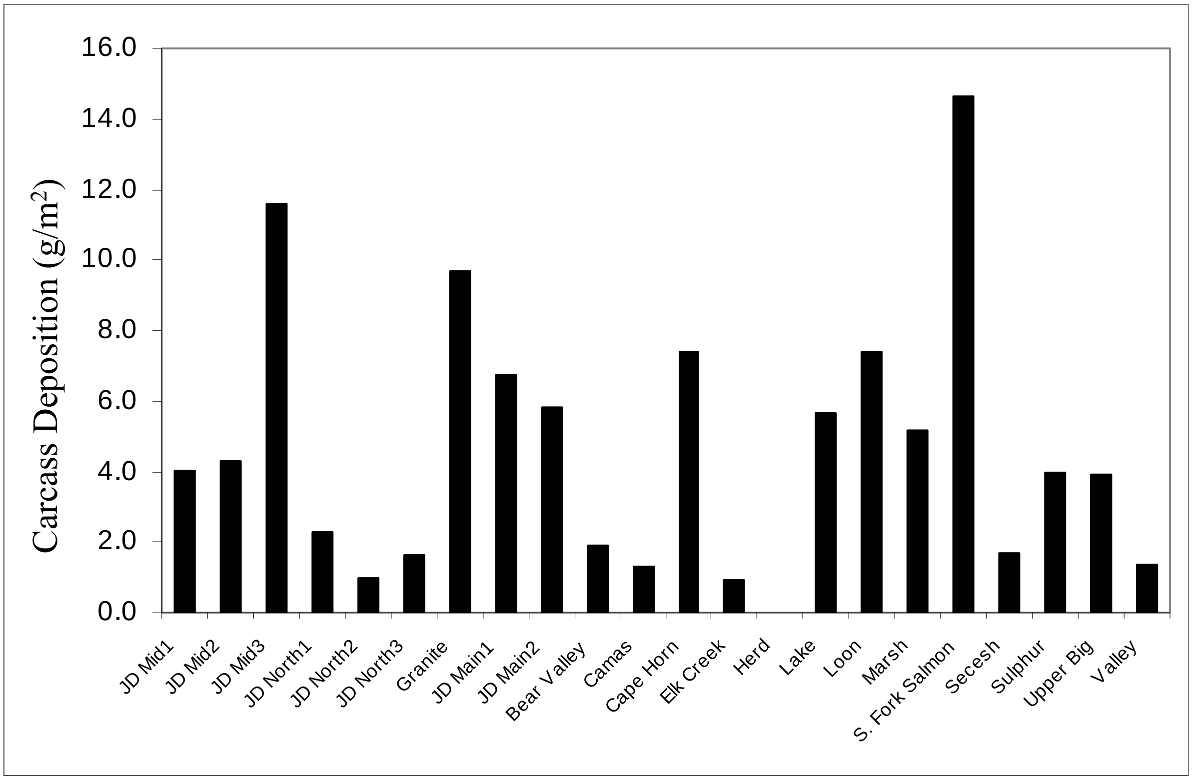
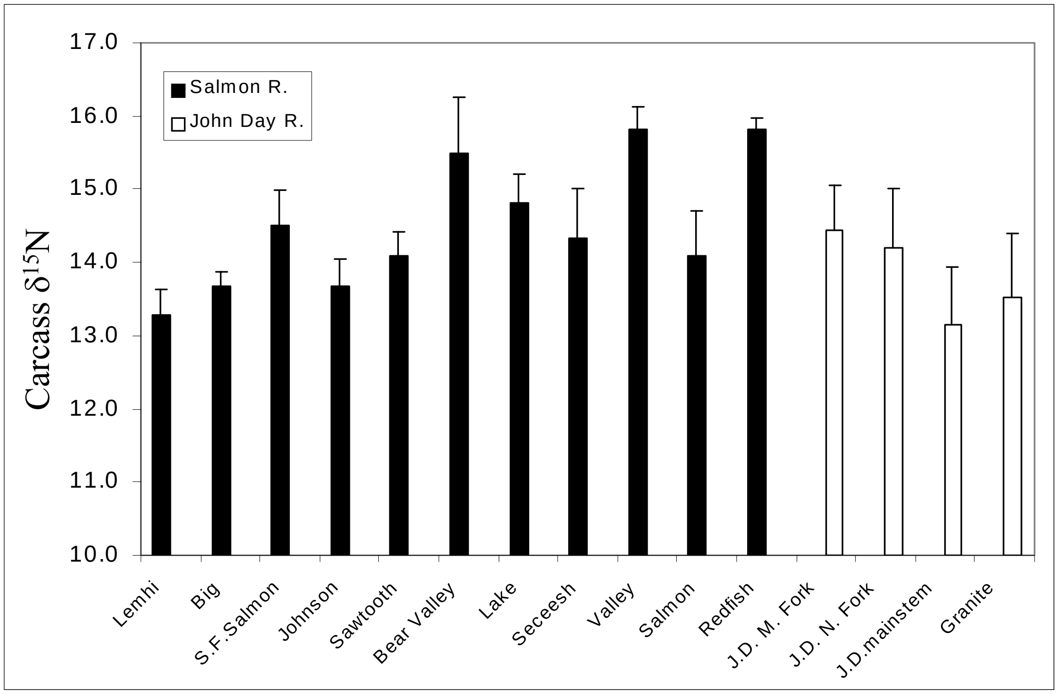

A. Study streams in the Salmon River basin, Idaho
Salmon R
Lake
Willow
Threemile
Nethker
SF Salmon R
Secesh
Logan
Big
MF Salmon R
Salmon R
Area of Detail
Rush
Camas
Lemhi R
Goat
Loon
Sulphur
Elk
Marsh
Pahsimeroi R
Valley
Salmon R
Cape
Horn
Bear
Valley
EF Salmon R
N
30
0
30
km
B. Study streams in the John Day River basin, Oregon
NF John Day R
John Day R
Granite
Clear
Bull Run
MF John Day R
Area of Detail
Reynolds
SF John Day R
20
0
20
40
km

Figure 1



Carcass Deposition (g/m^2)
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
JD Mid1
JD Mid2
JD Mid3
JD North1
JD North2
JD North3
Granite
JD Main1
JD Main2
Bear Valley
Camas
Cape Horn
Elk Creek
Herd
Lake
Loon
Marsh
S. Fork Salmon
Secesh
Sulphur
Upper Big
Valley

Figure 2



Salmon R.
John Day R.
Carcass δ15N
17.0
16.0
15.0
14.0
13.0
12.0
11.0
10.0
Lemhi
Big
S.F.Salmon
Johnson
Sawtooth
Bear Valley
Lake
Seceesh
Valley
Salmon
Redfish
J.D. M. Fork
J.D. N. Fork
J.D.mainstem
Granite

Figure 3

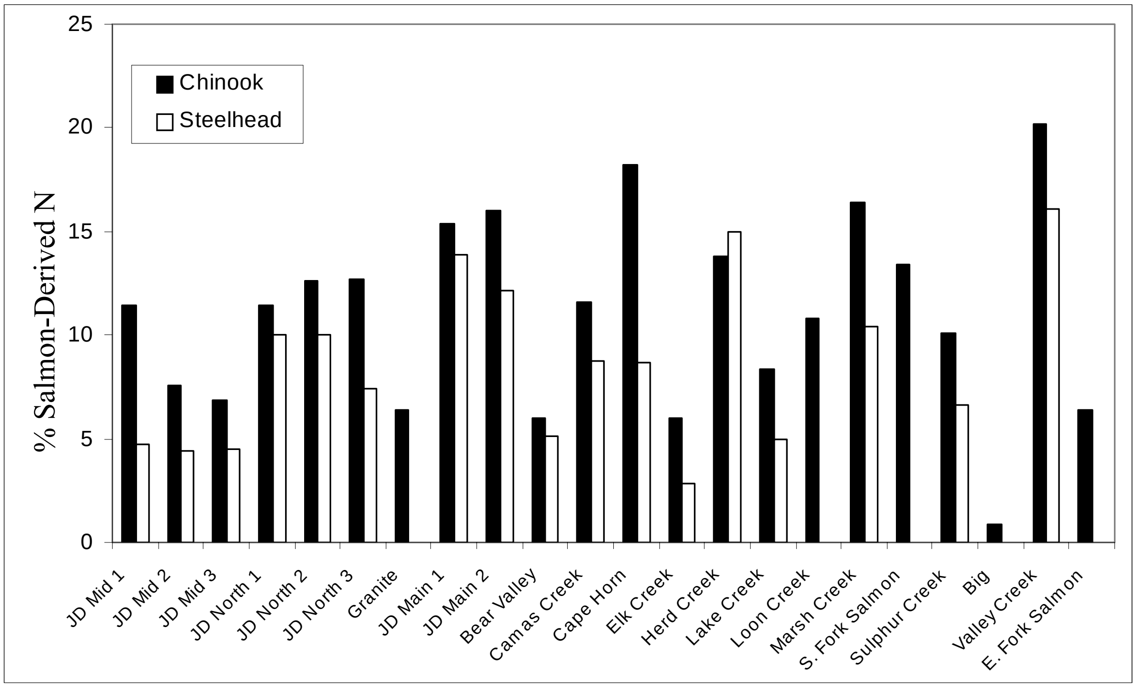
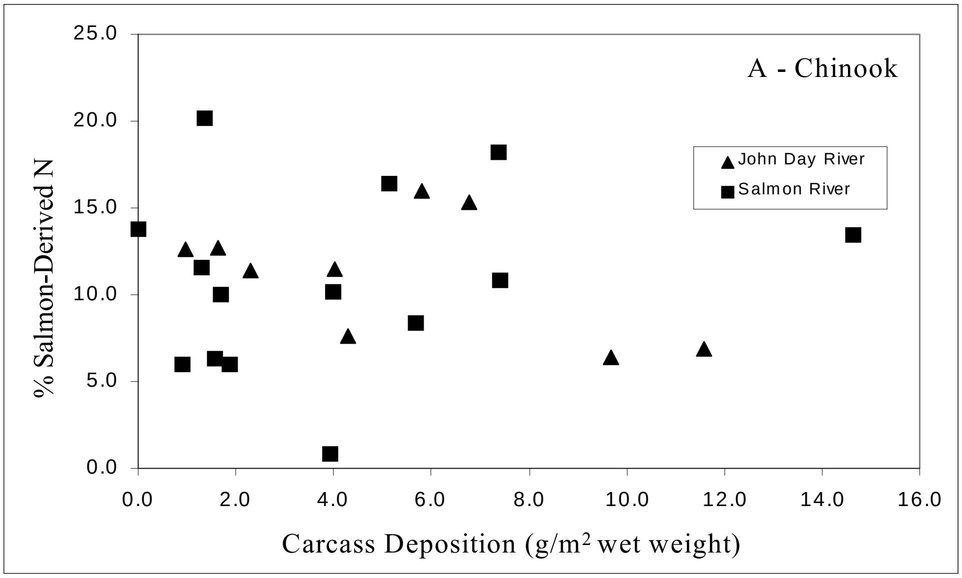

% Salmon-Derived N
25
20
15
10
5
0
Chinook
Steelhead
JD Mid 1
JD Mid 2
JD Mid 3
JD North 1
JD North 2
JD North 3
Granite
JD Main 1
JD Main 2
Bear Valley
Camas Creek
Cape Horn
Elk Creek
Herd Creek
Lake Creek
Loon Creek
Marsh Creek
S. Fork Salmon
Sulphur Creek
Big
Valley Creek
E. Fork Salmon

Figure 4


A - Chinook
John Day River
Salmon River
% Salmon-Derived N
25.0
20.0
15.0
10.0
5.0
0.0
0.0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
Carcass Deposition (g/m2 wet weight)

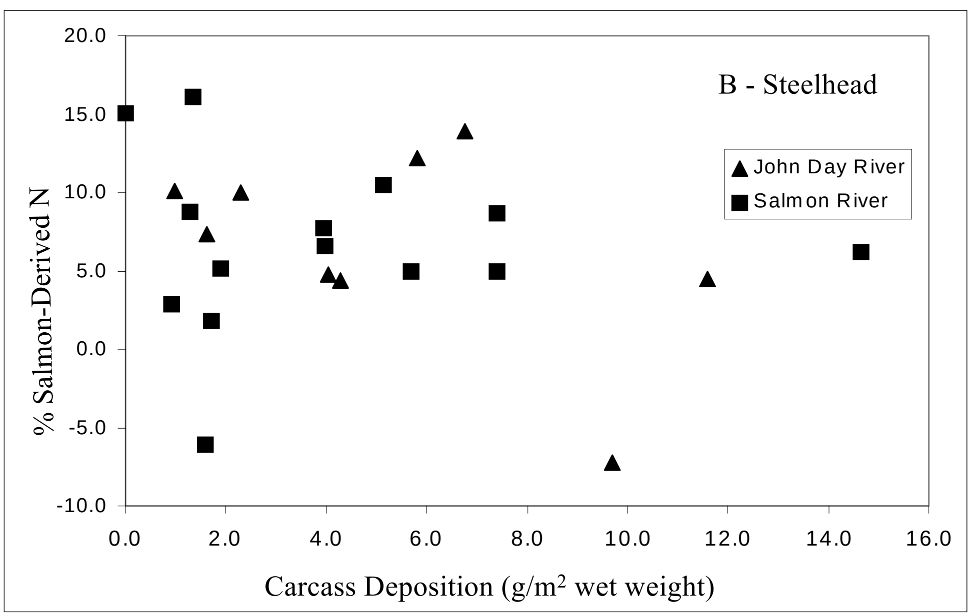
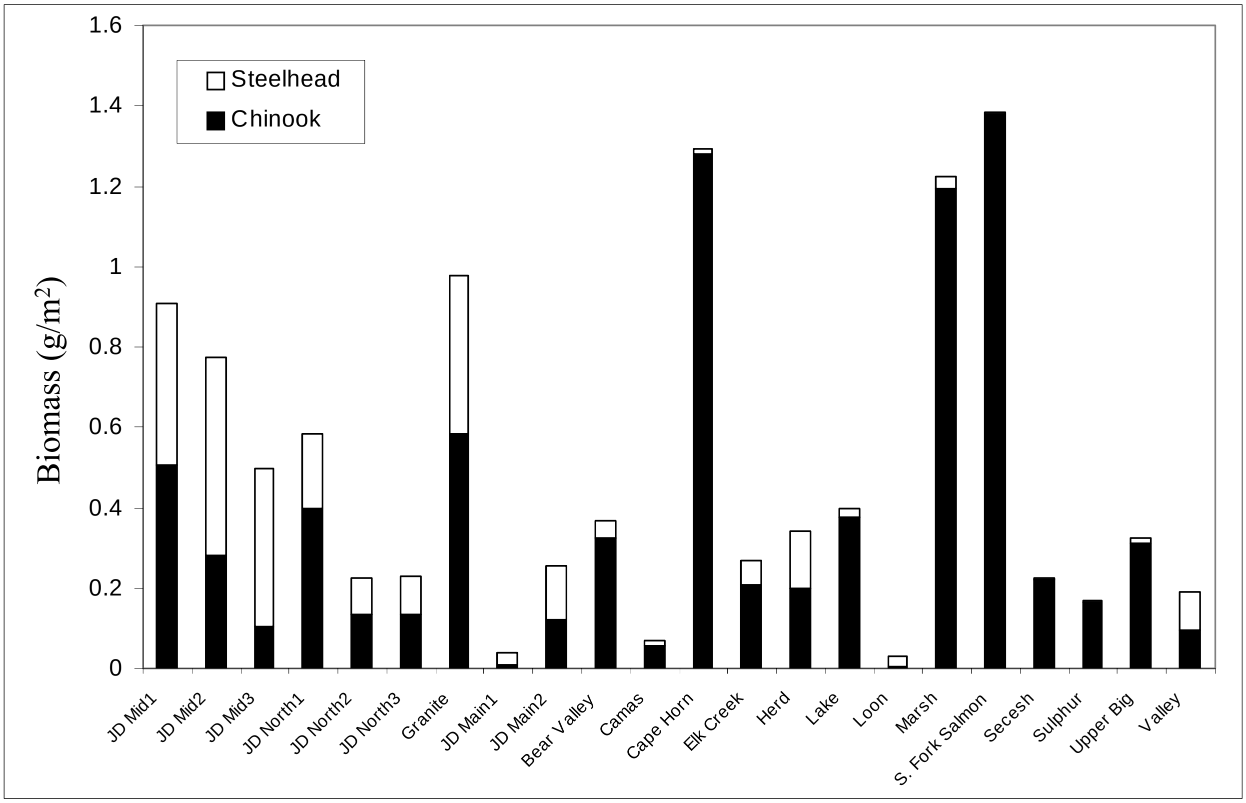
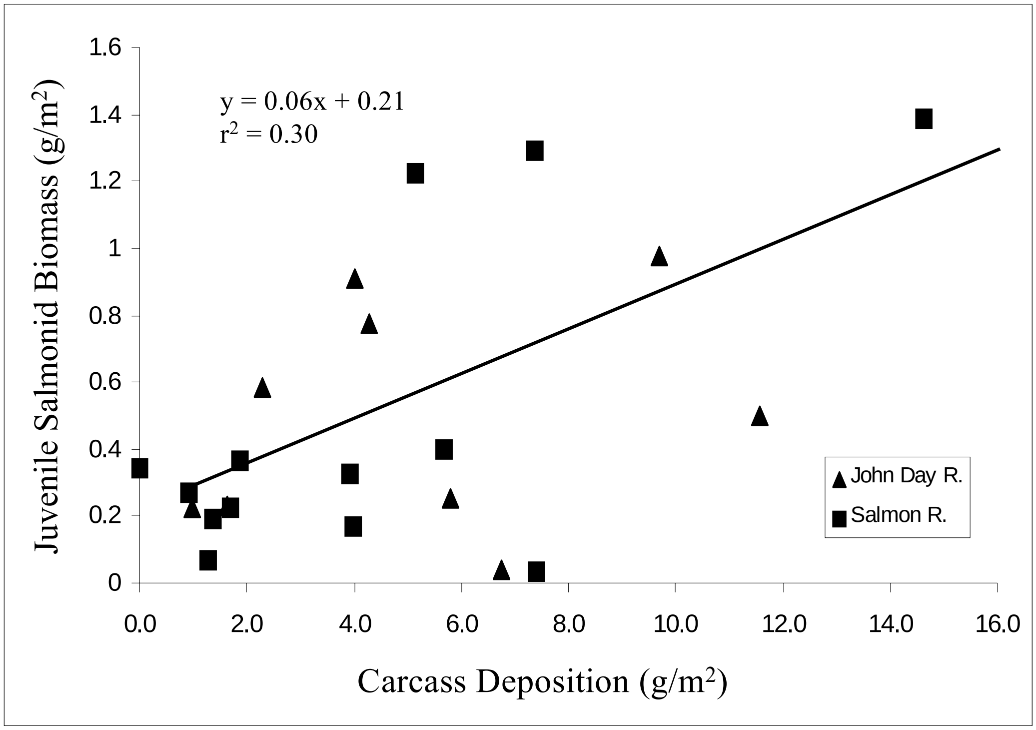

B - Steelhead
John Day River
Salmon River
% Salmon-Derived N
20.0
15.0
10.0
5.0
0.0
-5.0
-10.0
0.0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
Carcass Deposition (g/m2 wet weight)

Figure 5



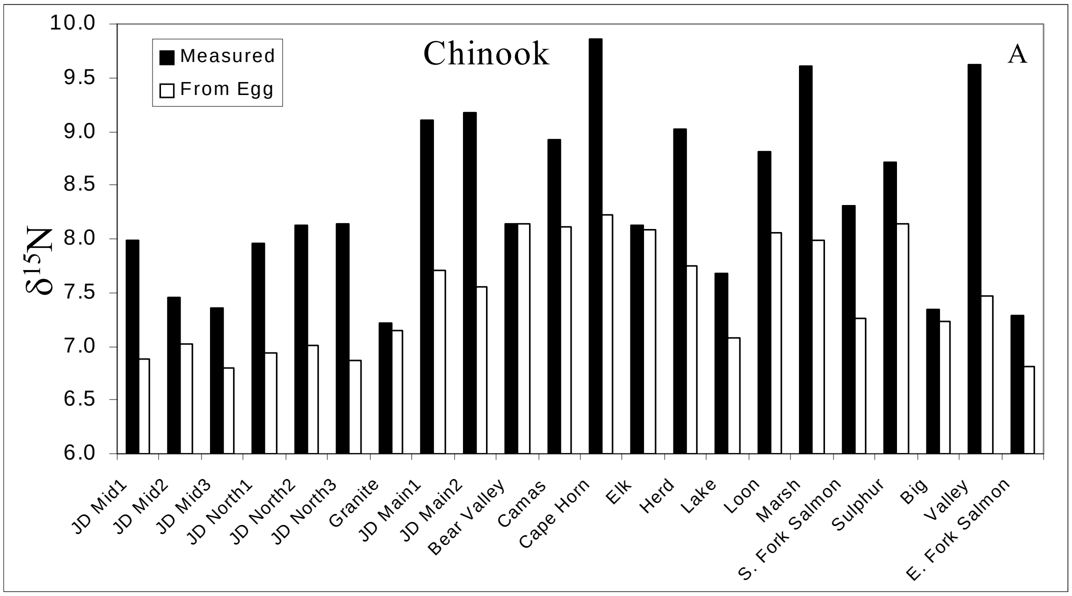
Biomass (g/m²)
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Steelhead
Chinook
JD Mid1
JD Mid2
JD Mid3
JD North1
JD North2
JD North3
Granite
JD Main1
JD Main2
Bear Valley
Camas
Cape Horn
Elk Creek
Herd
Lake
Loon
Marsh
S. Fork Salmon
Secesh
Sulphur
Upper Big
Valley

Figure 6

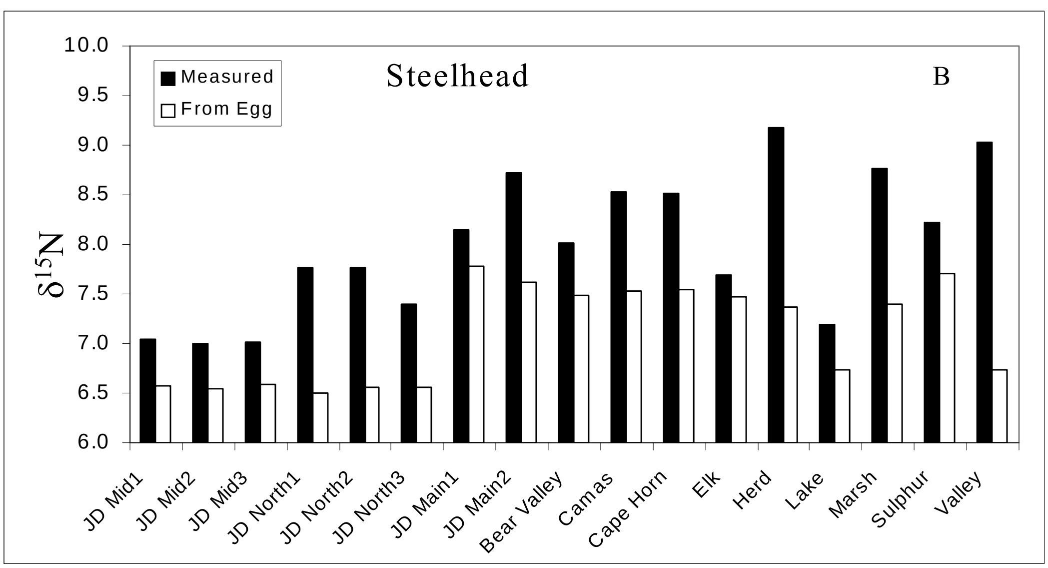


1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0.0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
y = 0.06x + 0.21
r2 = 0.30
Juvenile Salmonid Biomass (g/m2)
Carcass Deposition (g/m2)
John Day R.
Salmon R.

Figure 7



Chinook
A
Measured
From Egg
$\delta^{15}N$
10.0
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
JD Mid1
JD Mid2
JD Mid3
JD North1
JD North2
JD North3
Granite
JD Main1
JD Main2
Bear Valley
Camas
Cape Horn
Elk
Herd
Lake
Loon
Marsh
S. Fork Salmon
Sulphur
Big
Valley
E. Fork Salmon



Steelhead
B
Measured
From Egg
$\delta^{15}N$
10.0
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
JD Mid1
JD Mid2
JD Mid3
JD North1
JD North2
JD North3
JD Main1
JD Main2
Bear Valley
Camas
Cape Horn
Elk
Herd
Lake
Marsh
Sulphur
Valley

Figure 8